Growth with Age in the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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Growth with time of different sub-groups in the *Euastacus spinifer* population in two pools of the Loddon River has been measured and assessed. Annual increments of newly released juveniles maintained in captivity match predicted values from the linear regression calculated from large field samples (sub-adults, mature males <55mm CL). No difference in growth related to sex, could be detected and the decline in annual growth (again a linear relationship) for all specimens above 55mm CL is partially due to lowered moulting frequency, to a single annual moult.

Normal males mature at about 5 years (45–55mm CL), while females do not reach maturity until 8 years (~70mm CL) or older. Mean carapace length at age can be estimated with confidence up to at least 8 years; with calculated ages, for the largest specimens recorded at the study site, ranging from 22–39 years. Reports suggest that in some areas *E. spinifer* can attain a size (160mm CL) and weight (1.8kg) which place it among the largest of parastacid species.

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KEYWORDS: Annual growth, size at age, *Euastacus spinifer*, juvenile growth, maximum weight.

INTRODUCTION

The difficulties of determining age in crustaceans have been noted by many authors. But in the absence of ageing structures, growth rates may be determined by identifying age classes in catch size frequency distributions, or by following the growth of marked individuals. For relatively short-lived species, size at age can be estimated directly by the former method (Momot 1967; Weagle and Ozburn 1972) but in larger, long-lived species age classes may be obscured after the first few years by variable or low average growth rates (Bennett 1974; Chittleborough 1976; Farmer 1973). Then information on the age of larger individuals in wild populations can only be obtained through mark-recapture programs.

Size estimates at age can be made by combining the relationships of moult increment and frequency to body size (Bennett 1974; Berry 1971; Mauchline 1977). This combined method involves errors in fitting curves to two data sets and is only realistic when relationships, for moult increment and frequency, can be fitted by a single continuous curve, which is the case with *Euastacus spinifer* (Turvey and Merrick 1997c).

In this study on *E. spinifer*, annual growth rates have been estimated from the linear relationship between final carapace length after a twelve month period and initial carapace length, averaged for a number of individuals of different initial sizes. This estimated true growth may be used to calculate mean size at any age for surviving individuals, if mean size at one age covered by the calculated relationship is known. The reliability of size estimates drawn from these relationships depends upon the assumption that observed growth rates were typical of rates in previous years. The only other comprehensive studies relating *Euastacus* age to growth have been those on *E. bispinosus* (Honan and Mitchell 1995b). Objectives of this paper are: to measure annual growth rates in newly released juveniles, immature and mature samples of both sexes; to compare rates within and between these population sub-groups; to provide a series of estimates of size at age so that a total growth relationship relating carapace length with age in years can be developed; to relate age estimates with reproductive maturity, maximum individual size and longevity.

MATERIALS AND METHODS

The study site and techniques for sampling the Loddon River populations were documented in Turvey and Merrick (1997a,b). As there were no field recapture data for specimens below 20mm CL, growth at the smallest sizes was estimated from captive juvenile stocks.

Growth of Newly Released Juveniles

Mature females were collected just prior to the release of juveniles (November 1977). Mean CL of juveniles at release was estimated from a random sample (n = 20) measured before moulting, but after release from parents held briefly in aquaria. Females still carrying juveniles were introduced into a new, specially constructed farm dam in the adjacent Hacking River catchment; shelter and leaf litter was provided. In March 1978, 20 juveniles were removed from the dam and transferred to an outdoor tank (2.0 x 1.0m in area: depth 1.0m). The tank was aerated and juveniles supplied with shelters, leaf litter and detritus; small pieces of fish were added occasionally to supplement the diet.

This experimental stock was only disturbed three times during captivity and the tank was subjected to ambient temperature and photoperiod regimes. In November 1978 the trial was terminated and carapace lengths of the eight survivors measured (nearest 0.1mm). The differential between final carapace length (after one year) and initial CL was then compared with the relationship obtained for wild stocks.

Annual Growth Rate and Size at Age in Wild Populations

Annual growth increments, of *E. spinifer* at the study site, were measured using methods described in Turvey and Merrick (1997c). Carapace lengths after 12 months were plotted against initial lengths for annual increments of females and normal males of different sizes from Pools 3 and 7; no distinction was made between the data for males and immature females. Linear regressions of final CL after one year on initial CL were calculated separately for individuals with initial carapace lengths below and above 55mm; confidence limits (95%) for final lengths at any given initial CL were calculated for each regression and plotted as confidence belts. The regression line and confidence belts for individuals in the size range 20–55mm CL were extrapolated back to the estimated initial CL of captive juveniles, and compared with final lengths of these experimental stocks after approximately one year.

Using the mean CL of newly released juveniles as mean CL at age 0, the estimated CL at 12 months (age 1) may be read directly from the regression line described above; mean CL at two years of age may be estimated in a similar manner from the calculated mean size at one year. If the regression is linear, it is of the form,

$$L_{t+1} = a + bL_t$$

where L_{t+1} = final carapace length after one year and L_t = initial carapace length. Then the process of estimating consecutive sizes at age from the regression line generates a relationship of the form,

$$\frac{L_n = a(1 - b^n) + b^n L_0}{1 - b}$$

where L_n = mean carapace length after n years, L_0 = mean carapace length at age 0, providing that $b \neq 1$ (Kurata 1962). Separate equations of this form were constructed from the regression lines for individuals below and above 55mm CL. The first was applied up to and including the first mean CL at age that exceeded 55mm, and the second from this point onwards. Confidence limits (95%), calculated as for CL, were used to estimate approximate ranges of size at age for individuals.

In addition, the maximum carapace length attainable by a crayfish growing at a particular rate may be predicted from the regression line, as the point at which final CL equals initial length (assuming the relationship between the two variables remains unchanged). Maximum attainable lengths (with upper and lower 95% confidence limits), provided estimates of CL at age for individuals growing at the mean, sustained maximum and sustained minimum annual rates. These estimated attainable sizes together with the relationship between mean CL and age were compared to maximum carapace lengths recorded at the study site.

Relationship of Estimated Size at Age and Size Classes in Initial 1977 Catches

Size classes were determined for combined catches taken in May, June, July and August 1977 from both pools; a single size frequency distribution (CL class width 1mm) was constructed. Points of overlap of its constituent size classes were located using the probability paper method of Harding (1949); where feasible, the mean CL of individuals in each size class was calculated. The size distribution was plotted as a frequency histogram; the spacings and mean carapace lengths of contributing size classes were compared with the estimates of mean CL at age that had been derived from the mark-recapture data.

RESULTS

Growth of Newly Released Juveniles

The mean carapace length of juveniles at release was estimated to be 4.46mm ± 0.02mm (95% confidence limits). Carapace lengths of captive juveniles after approximately fifty weeks of growth, from the time of release from their mother were 10.8mm, 12.8mm, 12.8mm, 13.4mm, 14.4mm, 15.5mm, 17.0mm and 20.6mm.

Annual Growth Rate and Size at Age in Wild Populations

The relationship between carapace length after one year and initial length (Fig. 1) was closely approximated by a straight line for both size groups. The majority of final carapace lengths of the reared juveniles were grouped about the regression line for the group of smaller individuals (<55mm CL) and contained within the 95% confidence limits for the population at that point.

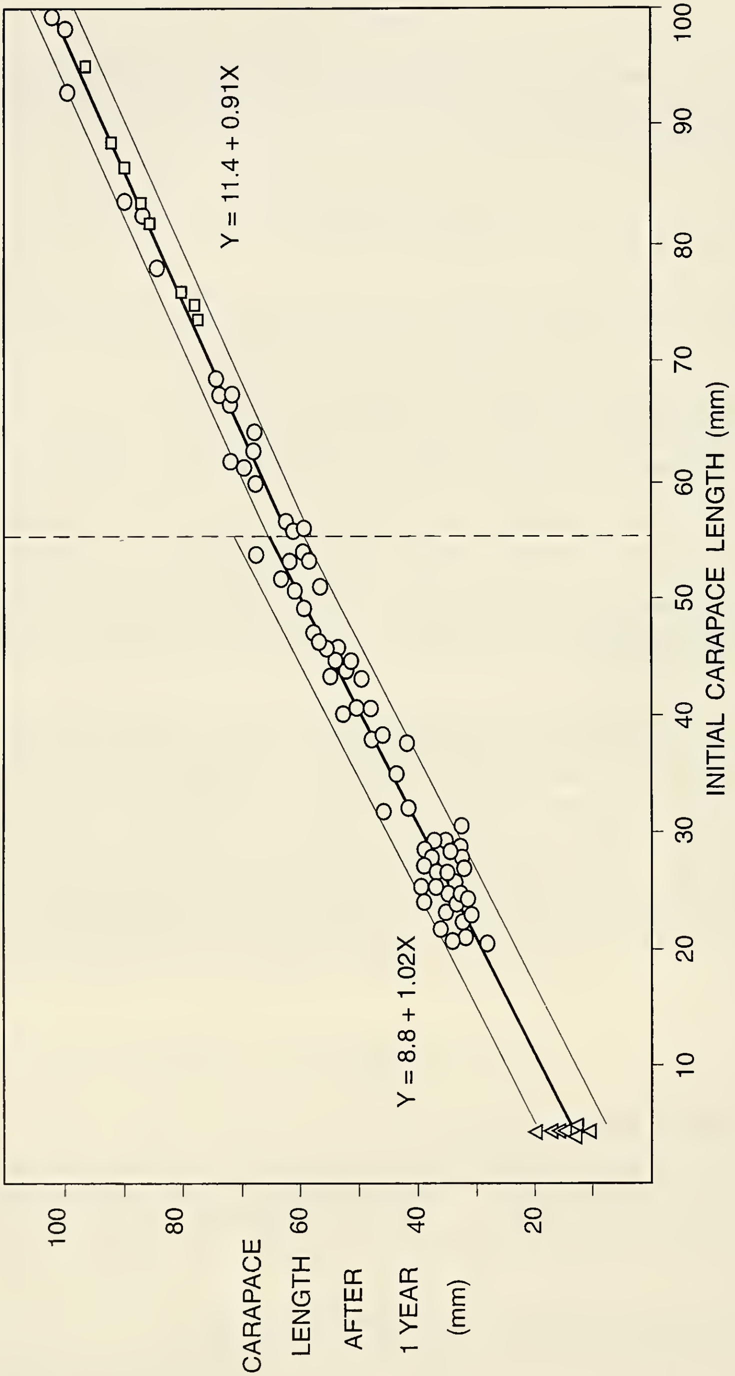

Figure 1. Relationship of carapace length after one year to initial carapace length in *E. spinifer*. Separate regressions have been fitted for individuals above and below 55mm CL; 95% confidence limits are for the population of carapace lengths after one year at any given initial carapace length. Key to symbols: Δ = juveniles raised in captivity; ○ = wild male or immature females; □ = wild mature females.

For individuals with initial carapace lengths exceeding 70mm, the final lengths of females were located on or just below the regression line, while the final lengths of males (and one immature female) were located above the regression line. The single exception was one of the largest males with a final carapace length below the regression line. The estimated maximum carapace lengths attainable by crays growing at the mean and sustained maximum and minimum annual growth rates were 123mm, 159mm and 89mm respectively. The predicted maximum carapace lengths of individuals growing at the estimated maximum and mean rates were both greater than the maximum recorded value at the study site.

Estimated mean carapace lengths increased exponentially with age up to a CL of 60.4mm at an age of six years (Fig. 2); however, the yearly increase in annual growth increments for these latter individuals was slight. For crays of ages greater than six years, annual growth increments decreased each year. The earlier attainment of a CL greater than 55mm, and subsequent adoption of the growth rate predicted for individuals sustaining the estimated maximum rate (60.4mm at 4 years), resulted in asymmetry of the maximum and minimum carapace lengths at age about the mean value for stock more than four years old.

Relationship of Estimated Size at Age and Size Classes in Initial 1977 Catches

The combined size frequency distribution was resolved into six size classes, up to a carapace length of 69mm (Fig. 3). The frequency distribution above this point consisted of a number of small, isolated groups which could not be identified reliably as discrete size classes. The mean CL of the size class containing the smallest crayfish was not calculated, as lower boundaries of this class could not be reliably determined. The spacing of the other size classes was similar to the spacing of the estimated mean carapace lengths of individuals at 3–7 years of age.

Estimated mean CL values at ages six and seven years were within 0.5mm of the size class means for individuals with carapace lengths exceeding 56mm. The mean CL of individuals in the 45–55mm size class was about 1mm less than the estimated mean carapace length for a five year old. The size class mean for specimens of 33–44mm CL was approximately 2mm less than the estimated mean CL for four year olds; the class mean for 25–33mm CL was about 4mm less than the estimated mean CL for 3 year olds.

DISCUSSION

The technique of estimating annual growth by CL differentials (averaged for samples of different size classes) was developed independently in this investigation; however, an earlier study (Hancock 1965) had also reported that this method provided a reliable assessment of true growth, providing that data were drawn from a number of age groups.

Growth

The experimental juveniles were maintained in conditions designed to approximate those in the wild and carapace lengths attained by these captives, after approximately one year, were generally close to the values predicted by the relationship determined for wild stocks. No distinction was made between values for immature females and males since moult increments and annual moult frequencies had been demonstrated to be the same (Turvey and Merrick 1997c). The pattern of differences in CL means, over five size classes and individuals 3–7 years old, conforms to that expected if growth rates during the study were typical of the growth in previous years.

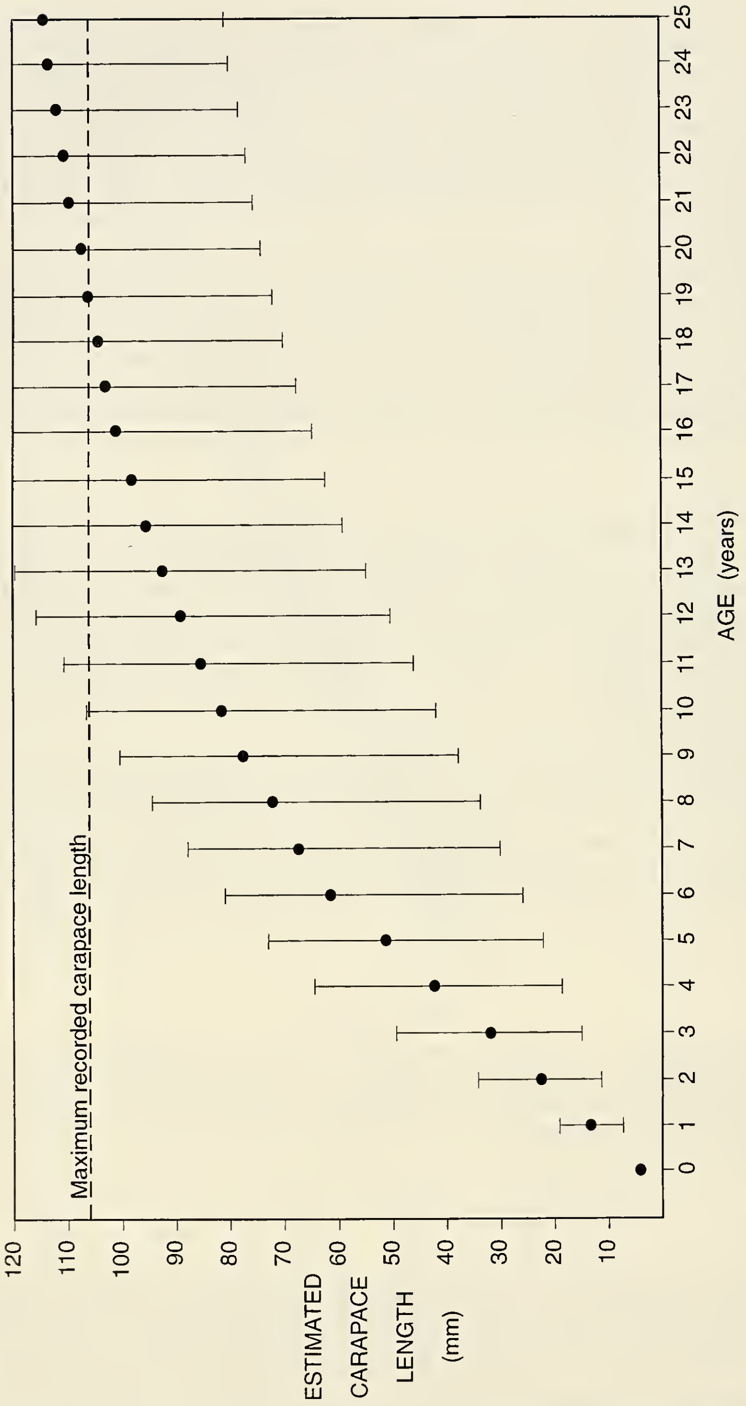

Figure 2. Estimated carapace length at age in *E. spinifer*. Key to symbols: ● = estimated carapace length at age for individuals growing at the mean annual rate; | = estimated carapace length at age for individuals sustaining the estimated maximum or minimum annual growth rate.

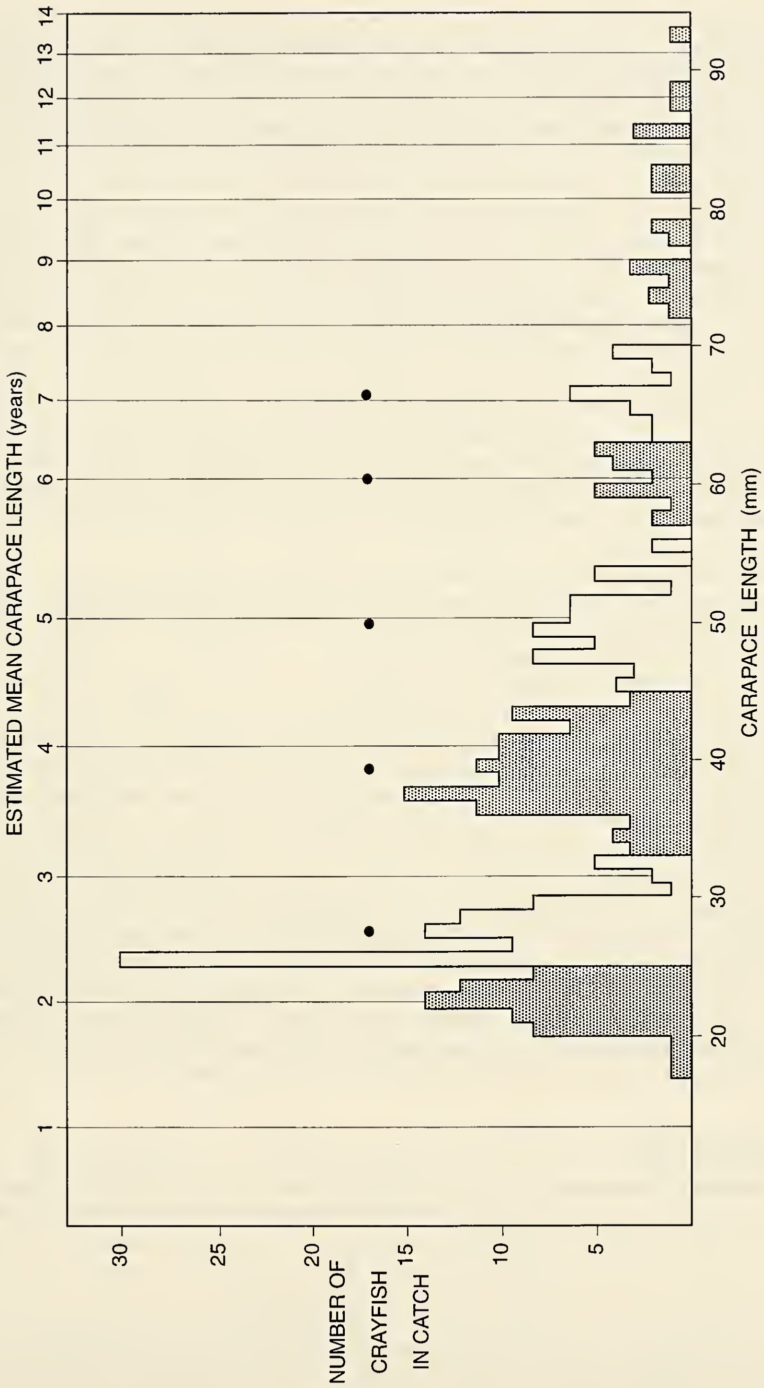

Figure 3. Relationship between estimated mean carapace length at age and size classes of *E. spinifer* in catches. Alternate size classes are distinguished by hatching; the size class containing the smallest individual is incomplete. Key: ● = mean CL of individuals in the size class.

The regressions (for <55mm and >55mm CL) were calculated separately for the following reasons. Individuals with carapace lengths just below 55mm typically moult twice per year, while individuals exceeding 55mm CL almost all moult only once per year. As moult increments of individuals with carapace lengths just below and for a considerable distance above 55mm are similar (Turvey and Merrick 1997c), an abrupt and sustained decrease, by a factor of about 50%, in the annual growth rates occurs at this point (Fig. 1).

The initial 1977 catches were selected for analysis of length classes for the following reasons. Firstly, as individuals rarely moulted during that period of the year (Turvey and Merrick 1997c), catches could be combined to provide a larger sample and more sensitive, reliable analysis. Secondly, the characteristics used to determine absence of moulting were independent of size; furthermore, size classes were determined from catches taken prior to any growth used to estimate annual rates from mark-recapture data.

If the difference between sampling time and end of the growth year is taken into account, the mean carapace lengths at age estimated from growth during the study coincide remarkably well with CL means of classes in 1977 catches. It can also be concluded that annual growth rates observed provide an accurate estimate of annual growth for at least seven years prior to these studies; this finding applies to specimens both greater and less than 55mm CL.

This conclusion has two implications: firstly, that mean CL at age can be confidently estimated for *E. spinifer* up to an age of at least eight years; secondly, that effects of environmental factors on growth were generally constant for at least eight years up to the end of the mark-recapture study.

Turvey and Merrick (1997c) found that sizes of consecutive moult increments were generally not correlated for any individual, so it is unlikely that any crayfish maintained the growth rates estimated from the 95% confidence limits for any protracted period. Sizes at age calculated from these growth rates must therefore be considered as potential maximum and minimum values that are unlikely to have been attained by *E. spinifer* in the study area, although they may have been reached by stocks in other areas.

Although samples of precocious males were too small for meaningful age analyses a brief discussion of preliminary findings is appropriate. The studies by Turvey (1980) indicated that this group, of very small but apparently sexually functional males, matured at ≥12mm (≥12 months age), declined in frequency when two or three years old (25–30mm CL) and a few survivors reached four years of age (~40mm CL). The suggestion that precocious males have similar growth rates to normal *E. spinifer* individuals contrasts with the situation in the freshwater prawn, where very small males are reported to have slow growth relative to other groups (Ra'anan et al. 1991).

Age and Life Cycle

Discussion relating age to life cycle events has to be in terms of estimated mean CL. The spread of carapace lengths about size class means (Fig. 3) indicated that most values in each class were within 5mm of the mean. So the age range for an individual of a given CL is likely to extend one year either side of the value indicated by the mean growth rate, for individuals up to ~60mm CL. This age range may increase as CL rises further due to variability in annual growth rates; but, broadening of the range is unlikely to be great, due to growth compensation. This process describes the interaction between higher growth of smaller individuals in a group and decreasing rates with increasing CL (Fig. 1), which causes a decrease in the spread of carapace lengths about a mean (Ricker 1975).

Average annual growth rates of mature females are typically smaller than those of males and the immature female of comparable size (Turvey and Merrick 1997c). If the relationship between final carapace length (after one year) and initial CL remained constant for very large individuals (an asymptotic approach to some theoretical maximum size), it is predicted that the maximum CL attainable by individuals growing at the mean rate would be approximately 123mm. This is considerably greater than the largest individual (♀: 105mm CL) measured during the study; however, several larger specimens were captured at the study site, with carapace lengths estimated at 110–120mm, so the predicted maximum size is probably realistic.

Based on the mean annual growth rate, specimens with carapace lengths of 110 and 120mm would be approximately 22 and 39 years of age respectively; an individual of 100mm CL would be 16–17 years old. These predicted ages must, however, be viewed with some caution. Given the probability of dying during any year at any size, it is suggested that individuals surviving to a large size may have been the more rapidly growing individuals. The situation described for *E. spinifer* is similar to that reported for large *E. bispinosus*, where apparently the data don't support either a hyperbolic or linear approach to maximum size (Honan and Mitchell 1995b).

Despite variability due to the above factors, a number of points relating to the age composition of Loddon River populations are clear. Individuals with carapace lengths over 110mm were present and specimens of ~100mm CL were not uncommon. It is unlikely that any of these large *E. spinifer* sustained growth in excess of the maximum rate calculated, for any protracted period, and minimal ages for individuals of 100 or 110 mm CL have been estimated at 10 and 12 years respectively (Fig. 2). This means that *E. spinifer* at the study site regularly reach 10 years of age. While the higher ages estimated for larger individuals are subject to some uncertainty, the considerable period of constant average growth prior to the study suggests that these ages (22–39 years) may not be unrealistic.

The minimum CL at maturity of female *E. spinifer* is approximately 70mm, while normal males mature over the range 45–55mm CL. These carapace lengths indicate ages at maturity of approximately 8 and 5 years respectively, similar to the situation demonstrated in *E. bispinosus* (Honan and Mitchell 1995b). As Table 1 shows, a number of *Euastacus* species apparently have this characteristic slow or late maturity (5–9 years) at a considerable size (CL >40mm).

There are reliable reports of *E. spinifer*, in other catchments near the study site, regularly reaching weights of about 1.8 kg. From the length-weight relationship determined from study samples (Turvey 1980), individuals of this weight would have a CL of approximately 160mm. This is close to the maximum attainable size predicted for sustained growth at the maximum annual rate at the study site. Furthermore, the average maximum size of *E. spinifer* in catches has been observed to vary considerably between locations, so there is no reason to doubt that *Euastacus spinifer* attains the weight range indicated.

As Table 1 shows only eight *Euastacus* species are known to reach 120 mm CL. A weight of 1.8kg would rank *E. spinifer* among the largest known species of freshwater crayfishes in the world, behind *Astacopsis gouldi* (<4.0kg), *Euastacus armatus* (3.0kg), *E. bispinosus* (2.6kg) and *E. hystricosus* (~2.5kg).

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TABLE 1

Summary of size, maturity and age data for 34 *Euastacus* species (from Honan and Mitchell 1995a,b; Merrick 1993; Morgan 1986, 1988, 1989, 1991, 1997).

Species	**Maturity Size (Age in years)**	**Maximum Size (CL in mm; Weight in kg)**
Euastacus armatus	♀40 *(6–9)	250 (3.0)
Euastacus australasiensis	♀30–40	~60
Euastacus balanensis	♀~30	35
Euastacus bidawalus	♀>40	50
Euastacus bispinosus	♀55–85 (8–11)	>130 (2.6)
Euastacus brachythorax	♀40–50	~50
Euastacus claytoni	♀40–50	~60
Euastacus crassus	♀50–60; ♂30–40	~60
Euastacus dangadi	♀ 30–40	~45
Euastacus dharawalus	♀~40	~60
Euastacus diversus	♀>40	50
Euastacus eungella	♀>30	50
Euastacus fleckeri	♀>80	130
Euastacus gamilaroi	♀~40	>40
Euastacus gumar	♀>30	>35
Euastacus hirsutus	♀30–40	~45
Euastacus hystricosus	♀~60; ♂~40	200(~2.5)†
Euastacus kershawi	♀65–70; ♂~50	~160
Euastacus neodiversus	♀40	55
Euastacus neohirsutus	♀30–40	~45
Euastacus polysetosus	♀~40	~55
Euastacus reductus	♀25–30	~35
Euastacus rieki	♀40–50	~55
Euastacus robertsi	♀>30	55
Euastacus setosus	♀30	40
Euastacus simplex	♀~40	~55
Euastacus spinichelatus	♀~30	~40
Euastacus spinifer	♀70 (7–8); ♂55 (5–6)	160 (1.8)
Euastacus sulcatus	♀40; ♂30	~120
Euastacus suttoni	♀40–60; ♂20	~80
Euastacus valentulus	♀40	125
Euastacus woiwuru	♀40–60	75
Euastacus yanga	♀30–50	>60
Euastacus yarraensis	♀40	~80

*All CL values are rounded (to nearest 5mm)

†Conservative weight estimate based on comparative size

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